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LONG-TERM EFFECTS OF DEFOLIATION ON RED PINE SUITABILITY TO INSECTS FEEDING ON DIVERSE PLANT TISSUES

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Abstract. Evidence that defoliation can induce long-term responses in perennial plants that can regulate insect population dynamics is based largely on studies using deciduous trees and folivores, particularly Lepidoptera. Studies with evergreen trees, and with insects feeding on other plant parts, have yielded more variable results. This study examined the effects over several seasons of controlled defoliation on the suitability of an evergreen conifer, red pine (*Pinus resinosa*) to insects and pathogens that exploit foliage, stem phloem, and root tissue. Test insects included a folivorous sawfly (Hymenoptera) and two species of stem- and root-colonizing beetles (Coleoptera). Each of these species undergoes periodic population irruptions.

Controlled defoliations were administered to 10-yr-old trees at levels that mimic naturally occurring sawfly outbreaks. Additional studies were conducted on seedlings in a glasshouse. Foliar suitability to the redheaded pine sawfly (*Neodiprion lecontei*) varied in a nonlinear fashion with defoliation intensity one year after treatment.

However, not all parameters of sawfly success were equally affected. Female cocoon mass was related to foliar concentrations of nutrients, but not monoterpenes or diterpene acids. Suitability to the stem boring pine engraver (*Ips pini*) increased 2 yr after defoliation. Moderate defoliation reduced stem resin flow rate by 50% and increased stem phloem colonization rate by the beetle's mutualistic fungus, *Ophiostoma ips.* Defoliation also affected host suitability to adult pales weevils, *Hylobius pales.* Weevil feeding increased 1 yr after defoliation, but this response dissipated 2 yr after treatment.

The observation that intermediate defoliation stress can either decrease or increase foliar suitability in an evergreen conifer, depending on intensity, is consistent with elements of both the plant stress and carbon : nutrient balance hypotheses. Moreover, host responses to a single stress agent may significantly and differentially influence the population dynamics of insects and pathogens that exploit different plant tissues. Implications of these results for plant stress and carbon : nutrient theories, plant-herbivore interactions, and chronic forest declines are discussed.

Key words: conifer; defoliation; forest decline; Hylobius; Ips; Neodiprion; Ophiostoma; Pinus; *plant–insect interactions; sawfly; stress.*

INTRODUCTION

Active tree responses to defoliation have been proposed as important factors regulating insect herbivore population dynamics (Rhoades 1985, Neuvonen et al. 1988, Rossiter et al. 1988, Karban and Myers 1989, Haukioja 1991, Faeth 1992*a*, *b*, Lundberg et al. 1994, Karban and Niiho 1995). Changes in host suitability can be affected by alterations in both allelochemical and nutritional constituents that impact the growth, survival, and fecundity of herbivores (Redak and Cates 1984, Clancy et al. 1988, Boecklen et al. 1991). Defoliation has been shown to induce a broad range of long-term impacts on subsequent insect generations (Bryant et al. 1991), including decreased suitability (Haukioja and Niemela 1979, Schultz and Baldwin 1982, Krause and Raffa 1992), no effect (Myers and Williams 1987, Haukioja 1991), or increased suitability (Niemela et al. 1984, Geri et al. 1988). The underlying bases for this enormous diversity are not clear. Some tree species have more commonly been shown to undergo active responses than others, but it is difficult to make generalizations because of differences in techniques, herbivore species, and underlying phytochemistry. Within species, foliar suitability can also be influenced by defoliation intensity (Wagner 1988, English-Loeb 1989, Hanhimaki 1989, Reich et al. 1993, Julkunentiitto et al. 1995, Krause and Raffa 1995), the type of defoliating agent (Krause and Raffa 1992), plant phenology (Haukioja 1991, Marquis 1992, Rathfon et al. 1993), and tree age (Karban 1987, Wagner 1986).

The wide diversity of responses among tree species may reflect general differences in carbon-allocation

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patterns between deciduous and evergreen species (Tuomi et al. 1988). Evergreen tree foliage has a higher ratio of carbon to nutrients, and a higher proportion of total stored biomass, than do deciduous trees (Bryant et al. 1983, Krause et al. 1993). Thus, Tuomi et al. (1988) hypothesized that defoliation of evergreens would reduce the carbon available for allelochemicals, without substantially affecting nutrient content, and thereby increase their suitability to herbivores. Conversely, deciduous trees would be more likely to exhibit decreased host suitability following defoliation. The available data with evergreen conifers (Niemela et al. 1984, Geri et al. 1988, Hanhimaki 1989, Lyttikainen 1992*a*, Raffa 1995), and deciduous angiosperms (Haukioja and Niemela 1979, Fowler and MacGarvin 1986, Schultz and Baldwin 1982, Clausen et al. 1991, Ruohomaki et al. 1996, Robison and Raffa 1997) generally support this view. In those instances where decreased suitability to subsequent folivores of evergreen trees has been observed following defoliation, it has most commonly occurred within growing seasons (e.g., Wagner and Evans 1985, Wagner 1986, Krause and Raffa 1995). Although the taxonomic unrelatedness between conifers and angiosperms lends a cautionary note to such comparisons, induced responses by deciduous *Larix* conifers are also consistent with this hypothesis (Baltensweiter et al. 1977, Krause and Raffa 1992, 1995, 1996).

Recent studies have considered effects of defoliation on host suitability to insects that exploit plant tissues other than foliage (Faeth 1986, 1991, Martin et al. 1994, Bauce and Carisey 1996, Rieske and Raffa 1998; Wallin and Raffa, *unpublished manuscript*). For example, defoliation can increase host suitability to stem-colonizing insects by reducing the carbon-based defenses required for primary and secondary resin accumulation in conifers (Wright et al. 1979, 1984, Raffa 1991). Again, however, it is difficult to make broad generalizations. The existing data do not allow us to evaluate the relative effects of defoliation on subsequent suitabilities to insects exploiting different host tissues, because of idiosyncracies inherent to each plant–herbivore system. Moreover, most studies addressing between-tissue effects have been conducted within a single season or with only one age class of tree. In this study, we report the effects of controlled defoliations of a common host plant against multiple insect groups across several growing seasons.

Red pine, *Pinus resinosa* Ait., is a shade-intolerant conifer extending from northeastern to upper-midwestern North America (Critchfield and Little 1966, McCune 1988). It possesses a combination of characteristics from several taxonomic groups within the genus, including long leaves, thick bark, small cones and seeds, and unarmed cones. Under optimal conditions, ovulate flowers appear at 5 yr, male flowers at 9 yr, and viable seed at 12 yr (Burns and Honkala 1990). This species shows quite low genetic heterogeneity compared to other gymnosperm and angiosperm trees (Fowler and Lester 1970). *Pinus resinosa* is widely planted in the Great Lakes region, where it is a predominant softwood species in commercial forests (Lindberg and Hovind 1985).

Conifer sawflies (Hymenoptera: Diprionidae) comprise the major folivore group exploiting *P. resinosa.* Sawflies include several irruptive species, whose populations periodically reach outbreak levels and can cause widespread host stress and mortality (Price et al. 1990, Haack and Mattson 1993, Larrson et al 1993). *Neodiprion lecontei* Fitch is a particularly irruptive species, frequently causing 100% defoliation (Benjamin 1955, Averill et al. 1982). In an extensive survey of forestry records from Wisconsin, Minnesota, Michigan, and Ontario, Haack and Mattson (1993) reported that each of these regions experienced ''heavy to severe defoliation'' by *N. lecontei* somewhere once every 2 yr over a 22–38 yr period. Thus, almost all host trees are exposed to severely defoliating populations at least a few times during their life span. *Neodiprion lecontei* is polyphagous (Shenefelt and Benjamin 1955, Larrson et al. 1993), feeding on *Pinus, Picea, Larix,* and *Cedrus* spp. throughout the eastern United States and southeastern Canada (Haack and Mattson 1993). Outbreaks typically develop from increased local populations on groups of adjacent trees. Adult females emerge from cocoons in the soil and oviposit in the needles of host trees (Codella and Raffa 1995*a*). Larvae feed gregariously, and unlike most conifer sawflies, feed on all foliar age classes. Larvae begin feeding at the tip of the needle and progress downward, leaving the sheath (Wilson et al. 1992). Individual larvae frequently move between host trees during development, including trees of different species. Defoliation can significantly alter the photosynthetic rates, carbohydrate production, and growth of red pine (Reich et al. 1993, Krause and Raffa 1996).

Ips pini (Say) (Coleoptera: Scolytidae) colonizes the primary stem phloem tissue of living trees. While entering their hosts, these beetles introduce the phytopathogenic fungus *Ophiostoma ips* (Rumb.) Nannp. In an earlier survey, we found *I. pini* to be the most significant stem colonizing insect of *P. resinosa* in Wisconsin, and all (or nearly all) beetles to be carriers of *O. ips* (Klepzig et al. 1991). *Pinus resinosa* can often resist attacks through a combination of carbon-based constitutive and inducible defenses, but successful colonization by this stem-colonizing complex is lethal to host trees (Raffa 1991, Raffa and Smalley 1995). *Ips pini* colonize all pine species in the Great Lakes region, and neither they nor their vectored fungi are reported to show any host race formation.

The belowground tissues of *P. resinosa* are colonized by a complex of weevils and bark beetles that partition the resource based on host morphology and physiology (Raffa 1996, Hoffman et al. 1997). The pales weevil *Hylobius pales* (Gerbst) (Coleoptera: Curculionidae) is

PLATE 1. *Neodiprion lecontei* larvae feeding on red pine foliage. Photograph by Greg Lintereur.

a major component of this complex, often occurs in association with bark beetles (Phillips 1990, Klepzig et al. 1991), and is a major pest of young pines throughout eastern North America (Lynch 1984). Adult weevils feed on stems and branches. Larval development by root-breeding weevils and their associated *Leptographium* fungi is rarely lethal to mature trees, but can predispose *P. resinosa* to subsequent attack by *I. pini–O. ips* complexes (Klepzig et al. 1995, 1996, Raffa and Klepzig 1996). Host suitability to *Hylobius* weevils can be affected by nitrogen level and microsite (Hunt et al. 1993).

In this study, we tested whether defoliation alters the suitability of *P. resinosa* to its principal insect herbivores exploiting various tissues over several growing seasons. In particular, we considered: (1) Does defoliation affect subsequent feeding, growth, and development by sawflies? (2) Does defoliation affect concentrations and allelochemicals of foliar nutrients? (3) Does host age affect tree responses to defoliation? (4) Does defoliation differentially affect suitability to insects and associated microorganisms that exploit separate plant parts and associated microorganisms?

MATERIALS AND METHODS

Parameters of host suitability to three insect herbivores, *Neodiprion lecontei*, *Ips pini*, and *Hylobius pales*, were measured on trees subjected to a range of controlled artificial defoliation treatments. *N. lecontei* larval feeding and development were measured on trees and seedlings to assess foliar responses to defoliation. Suitability to *I. pini–O. ips* complexes was assayed by measuring stem resinosis in response to a mechanical wound, and lesion formation in response to fungal inoculation. Suitability to the stem-feeding, root-breeding weevil, *H. pales*, was measured in feeding and oviposition assays.

All assay insects were derived from field collected populations that had developed for at least one generation on *P. resinosa*.

Tree culture and experimental treatment

Field treatments were conducted at a 0.5-ha plantation of 10-yr-old *P. resinosa* at the Coulee Experimental Forest, LaCrosse County, Wisconsin, USA (Township 24N, Range 5W, Section 18). Trees were grown from a common seed source, at the Wisconsin Department of Natural Resources seed orchard in Boscobel, Wisconsin. Trees were planted in sandy loam soil in rows spaced at 2-m intervals. Tree height averaged 2.51 $\pm$ 0.03 m (mean $\pm$ 1 SE, $n = 80$ trees) at the time of treatment. No significant natural defoliation had occurred in this plantation prior to the experimental treatments.

Treatments were applied as a randomized complete block. The treatments consisted of various levels of defoliation: 0% (control), 33%, 66%, 66% conducted on two occasions (33% each, separated by 30 d), and 99% (conducted as one 66% defoliation followed by a 33% defoliation 30 d later). Each treatment was applied to 16 trees. Percentage defoliation was based on the proportion of each needle removed. We used this method to facilitate comparisons with studies on other *Pinus–Neodiprion* systems (e.g., Wagner 1986), and because previous studies showed that this method generates relatively uniform growth responses in *P. resinosa* (Kulman 1965). Treatments were applied using hand shears. Previous studies demonstrated similar responses to natural vs. artificial defoliation methods among *P. resinosa* (Krause and Raffa 1995) and other evergreen conifers (Lyytikainen 1992*b*, Sanchez-Martinez and Wagner 1994), even though deciduous species may be more sensitive to the agent of defoliation (Hartley and Lawton 1987, Neuvonen et al. 1987, Baldwin 1990, Krause and Raffa 1992). Defoliation treatments occurred between 13 June and 3 July, 1986 during the shoot growth period. The second defoliation treatment occurred between 23 July and 3 August after shoot growth had ceased.

Greenhouse treatments were applied to seedlings that originated from the Wisconsin Department of Natural

Resources nursery, at Boscobel, Wisconsin. In October 1986, 120 three-yr-old *P. resinosa* seedlings were bare-root lifted and placed in dark cool storage at 4–5°C. In March 1987, seedlings were planted in 5-L plastic pots containing autoclaved quartz sand, field soil, compost, and sphagnum peat in a 7:1:1:1 ratio. Seedlings were cultivated in a glasshouse under ambient temperatures (20–30°C), and watered regularly with a fertilizer solution of 20% ammoniacal nitrogen, 20% available phosphoric acid, and 20% potash to maintain soil at a pH of 5–6. Natural light was supplemented with 400-W sodium vapor lamps 8–12 h/d.

In August 1987, 30 *P. resinosa* seedlings were randomly assigned to each of these four defoliation treatments: 0, 25, 50, and 75% of each needle removed, using hand shears. Seedlings were kept in the glasshouse under natural lighting and temperatures of 0–2°C for the winter. In spring, water and nutrients were provided to supplement ambient temperatures and aid bud break prior to insect assays. One-half of the seedlings were used in the insect bioassays reported here, and one-half were analyzed for effects on *P. resinosa* physiology, carbon allocation, and levels of total nonstructural carbohydrates, reported in Reich et al. (1993).

Effects of defoliation on foliar nutrients

The effects of defoliation on subsequent year foliar nutrient content were measured using three defoliation treatments (0, 33, and 66%) on five randomly selected blocks of the 10-yr-old trees in the field. In August 1987, 1 yr after defoliation, needles (20 g fresh mass) from current year shoots were collected and immediately frozen on dry ice until laboratory analysis.

Foliar nutrients were analyzed in early season current year foliage, 1 yr after defoliation. Samples were collected during the sawfly larval bioassay and analyzed for macronutrients (nitrogen, phosphorus, potassium, calcium, magnesium, and sulphur) and micronutrients (zinc, boron, manganese, iron, copper, aluminum, and sodium).

Nutrient concentrations were determined by the University of Wisconsin–Madison Soil and Plant Analysis Laboratory. Quantities were determined using an inductively coupled Plasma Emission Spectrophotometer, Model 34000 ARL (Applied Research Laboratories) coupled with a DEC (Digital Equipment Corporation) PDP 11/34 computer (Schulte et al. 1987). Percentage nitrogen was analyzed using a semimicro Kjeldahl procedure (Schulte et al. 1987). Micronutrients were expressed as milligrams per kilogram, and macronutrients as percent of dry mass.

Statistical analyses of macro- and micronutrients were performed using two-way multivariate analysis of variance (MANOVA) (Abacus Concepts 1989). Two MANOVA models were used to determine the effects of treatment and experimental block on each nutrient group. Univariate ANOVA was performed for each dependent variable if the overall MANOVA was significant at the $P < 0.05$ level using the Wilks' Lambda test (Abacus Concepts 1989). Mean separations were performed using Fisher's protected LSD test. Individual trees were used as experimental units.

Effects of defoliation, and host terpenoids, on larval sawfly performance

N. lecontei were collected as eggs from *P. resinosa* trees in Dane County, Wisconsin, USA in 1987. Fresh foliage shoots were held in water vials, and fed to larvae in growth chambers at 21–23°C, under a 18:6 light : dark (L:D) cycle. Additional *N. lecontei* for the seedling assays were collected as eggs from *P. elliottii* var. *elliottii* in Clay County, Florida, USA in March 1988. After hatch, these larvae were reared for one generation on *P. resinosa* foliage prior to their use in assays. Cocoons were carefully packed in moist sphagnum moss at 21–23°C for 3–6 wk until adult emergence. In the second generation, *N. lecontei* adults and larvae were provided fresh *P. resinosa* foliage shoots for oviposition and feeding, respectively.

N. lecontei larval development, pupal survival, and female fecundity were measured on test trees in the field 1 yr after defoliation. Larvae were reared in branch sleeve cages to prevent dispersal and predation. Dacron polyester sleeve cages ($0.2-m^3$ volume) were placed on three randomly selected branches per tree in July. Ten second instar larvae (10-d-old) were placed in each cage, and allowed to develop and spin cocoons. After 10 wk, cages were opened and the cocoons were collected, counted, and weighed (± 0.1 mg fresh mass). Cocoons were then stored in moist sphagnum moss and chilled at 15°C for 14 d, 2–4°C for 100 d, and finally returned to 15°C for 14 d to induce pupation. Cocoons were then held at 20°C until adult emergence to measure survival. Female fecundity was determined by dissecting a subsample within 24 h of adult emergence and counting the number of eggs.

Dependent variables were transformed to logarithms and analyzed using two-way (treatment, block) and one-way (treatment) analysis of variance (ANOVA; SAS Institute 1985). Mean separations were performed using Fischer's protected least significant difference tests at the $P < 0.05$ level. Mean female and male cocoon mass data were analyzed on a per-tree basis. Linear and quadratic regression analyses were conducted using Statview (Abacus Concepts 1992).

Seedlings were tested for foliar suitability to *N. lecontei* larvae 1 yr after defoliation. Two fourth instar larvae were weighed and then placed in a transparent plastic box ($21.5 \times 6.5 \times 6.0$ cm) with foliage from one seedling. A bouquet of 10 current-year needles held in a water vial was provided for each pair of larvae. Assays were conducted in a growth chamber at 22–23°C, 55–60% RH, and constant light. After 48 h, larvae, needles, and frass were collected, dried at 70°C for 72 h, and weighed. Five nutritional indices (Wald-

bauer 1968) were determined gravimetrically on a dry-mass basis (all masses in milligrams, time in days): relative growth rate (RGR, =mass gain/[mean body mass × time]); relative consumption rate (RCR, =[mass of foliage ingested]/[mean body mass × time]); efficiency of converting ingested food to biomass (ECI, =100 × mass gain/foliage mass ingested); efficiency of converting digested food to biomass (ECD, =100 × mass gain × [mass of foliage ingested − mass of feces]); and approximate digestibility (AD, =100 × [mass of foliage ingested − mass of feces]/mass of foliage ingested). Digestibility values (as percentages) were arcsine-transformed to correct heteroscedasticity of variances. There were 12–14 replicates of each measurement. Each index was analyzed using one-way ANOVA and LSMEANS procedures (Abacus Concepts 1989).

To determine the relationship between *N. lecontei* larval fresh and dry mass, in a preliminary experiment $n = 49$ healthy fourth and fifth instar larvae were weighed, dried at 70°C for 72 h, and reweighed. Another preliminary experiment demonstrated a strong linear relationship between fresh and dry larval masses: dry mass = 0.187 × fresh mass − 0.547 ($P < 0.0001$; $r^2 = 0.92$).

Six trees were assayed for foliar monoterpenes and diterpene acids during the sawfly bioassay and 45 female cocoons were collected from these trees. Individual insects were used as the experimental unit since the question of interest in this assay was how foliar chemistry affects cocoon mass (as opposed to how defoliation may affect foliar chemistry).

Foliar monoterpene and resin acid compositions were determined by gas liquid chromatography using the methods of Raffa and Steffeck (1988) and Foster and Zinkel (1982), respectively. Crushed foliage was extracted in analytical grade pentane containing 0.01% *p*-cymene internal standard for 24 h, and separated on a 25 m × 0.25 mm bonded fused silica open tubular polyethylene glycol column (Carbowax 20; Alltech, Deerfield, Illinois). Injector and detector temperatures were 225°C. Oven temperature was set at 60°C for 10 min and increased at 10°C/min to 160°C. Helium carrier gas flow rate was 30 cm/s. For resin acid analysis, pentane extracts were evaporated under a nitrogen gas stream, and the residue was diluted in a diethyl ether : methanol : water mixture 79:20:1 by volume. After isolation on a DEAE-Sephadex ion exchange column, the solution was evaporated under a stream of nitrogen gas and the residue was dissolved in 10 mL of methyl heptadecanoate internal standard and derivatized to its methyl ester form with diazomethane. The solution was concentrated under a nitrogen gas stream and passed through a nonpolar column (BDS; Supelco, Bellafonte, Pennsylvania). Injector and detector temperatures were 225°C. The oven temperature was set at 185°C for 15 min then increased by 1.5°C/min to 220°C, where it remained for 21 min. Identifications were determined based on prior analyses (Raffa and Steffeck 1988, Codella and Raffa 1995*b*, Klepzig et al. 1995), and by comparing retention times, relative to the internal standards, with retention times of analytical grade standards. Quantitative analysis was conducted by comparing the peak areas with internal standards.

Potential influences of foliar compounds on cocoon mass were analyzed using correlation, and stepwise and multiple linear regression techniques (Chatterjee and Price 1977, Abacus Concepts 1989). Correlation coefficients were calculated to determine the association between cocoon mass and each independent variable, and provide a measure of collinearity among independent variables. Correlation coefficients were evaluated by Fisher's *r* to *z* test. Since the independent variables were generally noncollinear, stepwise regression was conducted for each group of compounds (Chatterjee and Price 1977). Forward selection and backward elimination stepwise regression procedures were used on each plant compound group to develop the best models for female sawfly cocoon mass dependence on micronutrients, macronutrients, and terpenoids. Results from these procedures were essentially identical. The significant variables were then combined in a multiple regression analysis to determine a final model of the cocoon mass response to foliar chemistry (Abacus Concepts 1989).

Effects of defoliation on P. resinosa *suitability to bark beetle–fungal complexes*

Two years after defoliation, two parameters of host resistance to *I. pini–O. ips* complexes were measured: stem resin flow and fungal colonization (Raffa 1991, Raffa and Smalley 1995). Trees that were defoliated a total of 66% (33+33%), and controls, were assayed on 11 August 1988. Resin flow was measured from three 9.5 mm diameter holes drilled into each stem 1.4 m above ground. A 36-mL vial was fit snugly into the hole to collect resin. The vials were collected after 24 h, and resin flow (in grams) was determined gravimetrically. Host colonization by *O. ips* was measured in an adjacent section of stem.

Ophiostoma ips spore suspensions were cultured on potato dextrose agar amended with 150 mg/kg novobiocin. Fungi were cultured in petri dishes under fluorescent lighting at 20–25°C for 5 to 7 d prior to inoculation (Klepzig et al. 1991, Raffa and Smalley 1995). The dishes were nearly completely colonized with mycelium at the time of inoculation. Fungi were originally isolated in pure culture (W20-84) in 1985 from adult *I. pini* that infested a dying *Pinus sylvestris* L., in Dane County, Wisconsin, USA.

Inoculations were performed by boring a hole to the sapwood with a 4 mm diameter cork borer, applying a mycelial plug to the sapwood using a 3 mm diameter metal syringe, and then replacing the bark (Raffa and Smalley 1995). Eight days after inoculation, the outer bark was removed to expose fungal lesions on the inner

TABLE 1. Effects of *Pinus resinosa* defoliation on subsequent year foliar nutrient concentrations (mean ± 1 SE).

Nutrient	Defoliation level (% of each needle removed) 0	33	66
Macronutrients (%)			
N	1.02 ± 0.03[a]	1.03 ± 0.04[a]	0.96 ± 0.01[b]
P	0.08 ± 0.01	0.09 ± 0.01	0.09 ± 0.01
K	0.39 ± 0.02	0.43 ± 0.02	0.41 ± 0.03
Ca	0.34 ± 0.04	0.39 ± 0.03	0.34 ± 0.03
Mg	0.11 ± 0.01	0.11 ± 0.01	0.10 ± 0.01
S	0.08 ± 0.01	0.07 ± 0.01	0.08 ± 0.01
Micronutrients (mg/kg)			
Zn	18.0 ± 2.4	19.1 ± 2.2	13.1 ± 3.0
B	12.7 ± 0.6	12.2 ± 1.1	11.1 ± 0.2
Mn	484.7 ± 51.4	571.2 ± 54.6	494.2 ± 27.3
Fe	57.6 ± 7.2	90.6 ± 39.6	77.7 ± 12.6
Cu	22.3 ± 8.7	36.7 ± 10.0	101.8 ± 52.2
Al	171.4 ± 41.9	168.5 ± 12.9	197.3 ± 27.6
Na	221.4 ± 19.1	208.7 ± 33.4	298.5 ± 74.4

Note: Different superscript letters within rows indicate statistical significance at $P < 0.05$.

phloem tissue. Lesion length was measured (±0.5 mm) on the phloem surface of the phloem–sapwood boundary. There were 11 replicates.

Mean resin quantity per tree was (log + 2) transformed, and analyzed using ANOVA. Lesion lengths were log transformed to standardize variances. The effects of defoliation on fungal colonization rates were analyzed using one-way ANOVA (Abacus Concepts 1989).

Effects of defoliation on P. resinosa *suitability to* H. pales

Hylobius pales adult weevils were obtained from a laboratory colony reared on *P. resinosa* stem bolts at 22°C and a 18:6 L:D photocycle (Hoffman and Raffa 1992). This colony originated from parental *H. pales* collected in Waushara County, Wisconsin using baited pitfall traps as described by Hunt and Raffa (1989), and was thereafter replenished annually with wild insects. Weevils were reared in 20-L plastic buckets with 10 cm of sterilized sand and a fresh 30–35 cm bolt cut from 20-yr-old trees. Freshly cut bolt ends were waxed to minimize desiccation. The colony received distilled water spritzes every 3–5 d to maintain adequate humidity. Adults were collected within 24 h of emergence for assays.

Two years after treatment, *H. pales* were offered pairs of same-aged twigs from 66% defoliated (33+33%) and control trees. In August 1988, six randomly selected 3-yr-old branchlets were sampled from three trees per treatment. One- and two-year-old twigs were divided into 7–10 cm sections. One female and one male adult weevil were offered a choice between the treatment and control twigs. Separate assays were conducted for each of the two twig section ages. In summary, there were 18 replicates of two twig years for defoliated or control trees, for a total of 72 weevils.

Twigs and weevils were held in a covered plastic box (21.5 × 6.5 × 6.0 cm) containing 1–2 cm of moist sand. Boxes were randomly assigned positions in an incubator at 22–23°C and 16:8 L:D. After 6 d, twigs were removed, and the number of feeding scars and eggs were counted. Effects of defoliation on weevil feeding and oviposition were analyzed for each year using two-tailed paired *t* tests. In a preliminary experiment to test the effect of twig age on weevil feeding preference, adults were simultaneously offered 1- and 2-yr-old twigs from the same control tree, using the above protocol. The number of feeding scars and eggs deposited were analyzed by ANOVA.

RESULTS

Effects of defoliation on foliar nutrients

Defoliation had significant but slight effects on the foliar nutrient content of *P. resinosa* 1 yr after treatment (Table 1). As a class, macronutrients showed a significant overall response (df = 12, 6; $F = 4.43$, $P < 0.039$). Among the individual macronutrients, nitrogen was most consistently affected, relative to controls ($F = 8.35$; df = 2, 8; $P < 0.011$). Nitrogen levels were reduced by ~6% in foliage from trees that had undergone 66% leaf removal. Two other macronutrients, phosphorus ($F = 3.50$; $P < 0.081$) and magnesium ($F = 3.12$; $P < 0.099$) were significantly affected at the $P < 0.1$ level. These macronutrients showed an increase of 13%, and a decrease of 9%, respectively.

Micronutrients, as a class, showed a significant overall response to defoliation (df = 14, 4; $F = 19.4$; $P < 0.006$), with the most common pattern being somewhat higher concentrations at the 33% defoliation treatment

TABLE 2. *Neodiprion lecontei* larval growth, consumption, and utilization of red pine seedling foliage one year after defoliation.

Defoliation (%)	RGR (mg·d^{-1}·mg^{-1})	RCR (mg·d^{-1}·mg^{-1})	ECI (% of DM)	ECD (% of DM)	AD (% of DM)
0	0.048[a] ± 0.02	2.7 ± 0.2	1.9[a] ± 0.4	14.9[a] ± 4.9	19.5 ± 3.7
25	0.049[a] ± 0.03	3.7 ± 0.4	1.5[a] ± 0.4	9.8[a] ± 1.9	16.0 ± 1.3
50	0.087[b] ± 0.04	3.3 ± 0.5	2.8[a,b] ± 0.3	28.6[b] ± 6.4	12.6 ± 1.2
75	0.093[b] ± 0.06	3.3 ± 0.5	3.9[b] ± 0.9	20.8[a,b] ± 6.5	14.9 ± 2.0

Notes: Larvae were fed current-year needles for 48 h. Data (mean ± 1 SE) within columns followed by different superscript letters are statistically significant ($P < 0.05$). See *Results: Effects of defoliation on* N. lecontei for explanation of abbreviations.

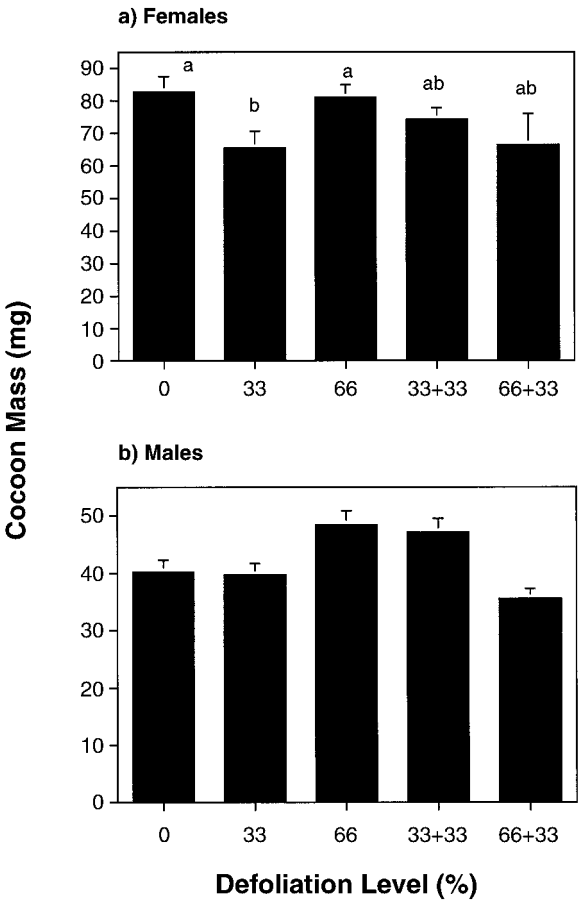

FIG. 1. Effects of defoliation (percentage of each needle removed) on masses of *Neodiprion lecontei* cocoons (fresh mass) following larval feeding on subsequent-year *Pinus resinosa* foliage. Bars (mean and 1 SE) with different letters are statistically significant at $P < 0.05$ (Fisher's protected LSD).

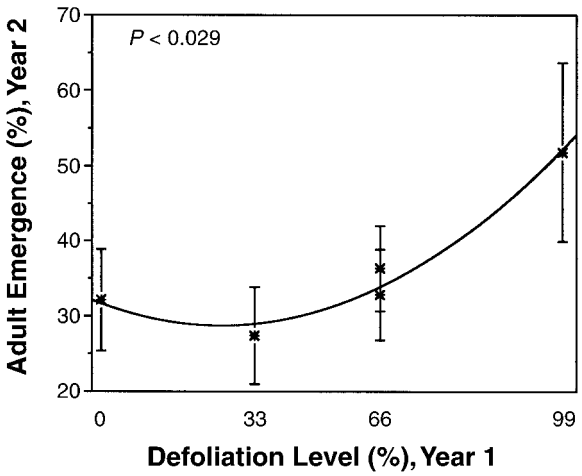

FIG. 2. Effects of defoliation on *Neodiprion lecontei* adult emergence following larval feeding on *Pinus resinosa* foliage one year after defoliation. Symbols (means ± 1 SE) show percentage adult emergence per tree.

(Table 2). However, no individual micronutrients were significantly affected by defoliation.

Foliar nutrients also varied within the pine plantation, presumably due to spatial differences in soil composition. Experimental block was a significant source of variation in overall foliar micronutrient ($F_{28,8} = 5.27$; $P < 0.006$), and to some extent, macronutrient ($F_{24,12} = 2.27$; $P < 0.07$) concentrations.

Effects of defoliation on N. lecontei

Defoliation affected the subsequent performance of *N. lecontei* larvae on *P. resinosa*. However, these responses were quite complex, and varied with the intensity of defoliation, the insect parameter, and host plant age.

On seedlings, larval relative growth rates (RGR) increased markedly with defoliation intensity one year after treatment ($F_{3,35} = 3.44$; $P < 0.03$) (Table 2). This response appeared to show a threshold, rather than linear relationship to defoliation intensity. A threshold appears to occur between 25% and 50%, defoliation and higher defoliation did not result in additional increases. Similar trends were observed for increases in efficiency of conversion of ingested food (ECI; $F_{3,39} = 2.98$; $P < 0.05$), and, to a lesser extent, in efficiency of conversion of digested food (ECD; $F_{3,36} = 2.24$; $P < 0.1$). Relative consumption rates (RCR) and approximate digestibility (AD) were not affected. These results suggest that foliar quality, rather than the amount of foliage ingested, is primarily responsible for *N. lecontei* larval growth rates. These differences in larval growth rates appear to reflect systemic whole-plant responses that influence new foliage, rather than just alterations in residual foliage, as new tissue comprised the majority of the food supply.

In the experiment on large, field growing trees, cocoon mass was affected by defoliation intensity 1 yr after defoliation, but the results varied with sex. In females, cocoon mass was reduced by ~21% (17.2 mg) in the trees that had been treated by 33% defoliation. At 66% defoliation, there was no treatment effect, and the most severe defoliations appeared to generate intermediate sized female cocoons. In males, the overall treatment effect was only significant at $P < 0.1$. However, there was a general trend for larger cocoons to be produced from larvae that fed on trees treated at the 66% defoliation level. For example, a single defoliation treatment of 66% yielded cocoons that were 8.2 mg larger than controls ($P < 0.1$). Among controls, female cocoons were approximately twice as large as males (Fig. 1).

Adult emergence from cocoons was affected by prior defoliation (Fig. 2). Emergence varied nonlinearly with defoliation intensity ($F_{2,2} = 34.32$, $P < 0.02$, $r^2 = 0.94$, $y = 0.004x^2 - 0.226x + 31.637$). Emergence declined following 33% defoliation, but steadily increased with higher defoliation intensities. This suggests an extend-

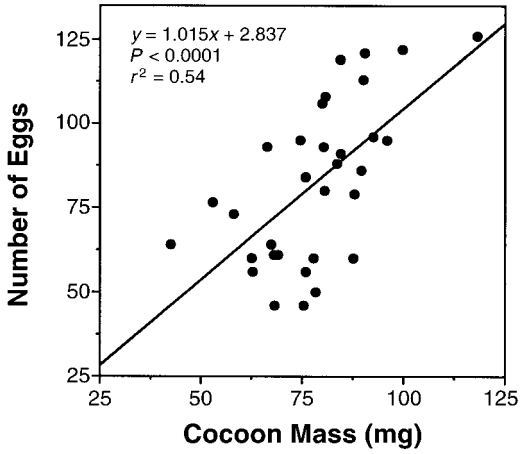

FIG. 3. Relationship of *Neodiprion lecontei* fecundity to cocoon mass ($F_{1,32} = 27.71$, $P < 0.0001$).

ed effect of host plant on nonfeeding life stages, since all pupae were incubated in a single environmental chamber.

Cocoon mass had a significant positive linear effect on female fecundity (Fig. 3) ($F_{1,32} = 27.71$, $P < 0.0001$). This relationship may have varied among treatments. The numbers of eggs per unit cocoon mass were 1.19 ± 0.07 eggs/mg [mean ± 1 SE] at 66% defoliation, 1.06 ± 0.1 eggs/mg at 33% defoliation, 0.97 ± 0.08 eggs/mg at zero defoliation, 0.97 ± 0.07 eggs/mg at 33+33% defoliation, and 0.85 ± 0.12 eggs/mg at 99% defoliation. However, sample sizes were not high enough to allow separate evaluations of female fecundity based on defoliation treatment. Predation by wood ants (*Formica montana*), even within sleeve cages, reduced sample sizes appreciably, and resulted in unbalanced data sets; combined with relatively low adult emergence at some defoliation intensities (Fig. 2), this resulted in insufficient sample sizes for analysis.

Simple linear regression indicated a strong association between cocoon mass and boron ($r^2 = 0.90$; $P < 0.002$) and calcium ($r^2 = 0.69$; $P < 0.04$), and a weaker relationship to zinc ($r^2 = 0.52$, $P < 0.1$). *Neodiprion lecontei* performance was not significantly correlated with concentrations of any other nutrient, total diterpene acids, or total monoterpenes. Results from the stepwise regression analyses for each chemical group indicate that three nutrients, phosphorus, magnesium, and boron, were significantly related to female sawfly cocoon mass. Combining the effects of phosphorus, magnesium, and boron into a multiple regression model indicates that together these compounds explain >56% of the variation in cocoon mass (Table 3A). In the reduced model, phosphorus, magnesium, and boron combine to yield a highly significant model of *N. lecontei* cocoon mass ($F_{3,41} = 17.02$; $P < 0.0001$, $r^2 = 0.55$) (Table 3B). No other nutrients, nor any of the monoterpenes or diterpene acids, were related to cocoon mass.

Effects of defoliation on I. pini–O. ips *complexes*

Defoliation reduced the parameters of *P. resinosa* resistance to stem-feeding insect–fungal complexes. Two years after 66% defoliation, stem resin flow rates were one-half those present in the control trees ($F_{1,19} = 4.9$; $P < 0.04$) (Fig. 4 top). Likewise, fungal colonization of phloem tissue was significantly more extensive on trees defoliated 66% than on controls ($F_{1,19} = 7.716$; $P < 0.02$) (Fig. 4 lower).

Effects of defoliation on P. resinosa *suitability to* H. pales

Defoliation increased the suitability of young pine twigs to adult *H. pales* increased on young pine twigs after defoliation (Fig. 5). In the two-way choice test, defoliation resulted in alterations in stem quality that doubled the number of feeding wounds on 10-yr-old

TABLE 3. Multiple regression analysis for effects of *P. resinosa* current-year foliar components on female *N. lecontei* cocoon mass ($n = 45$). Variables were first identified by using stepwise regressions to produce a full model (A), and reduced model (B).

Variable	Regression model				
	Coefficient	1 SE	Std. coeff.	*t*	*P*
A) Full model†					
Intercept	0.859	0.477	0.859	1.921	0.062
Phosphorus	6.021	3.292	0.477	1.829	0.075
Magnesium	−2.824	1.439	−0.937	−1.963	0.057
Boron	0.068	0.031	0.360	2.180	0.035
Copper	-3.5×10^{-6}	-3.2×10^{-4}	-2.2×10^{-3}	−0.11	0.991
Beta Pinene	4.1×10^{-3}	6.7×10^{-3}	0.498	0.603	0.550
Mycene	−0.011	0.20	−0.376	−0.579	0.566
B) Reduced model‡					
Intercept	1.028	0.325	1.028	3.160	0.003
Phosphorus	4.926	2.006	0.390	2.456	0.018
Magnesium	−2.225	0.567	−0.738	−3.928	0.0003
Boron	0.058	0.026	0.308	2.277	0.028

† $F_{6,38} = 8.24$, $r^2 = 0.565$, and $P < 0.001$.
‡ $F_{3,41} = 17.02$, $r^2 = 0.555$, and $P < 0.0001$.

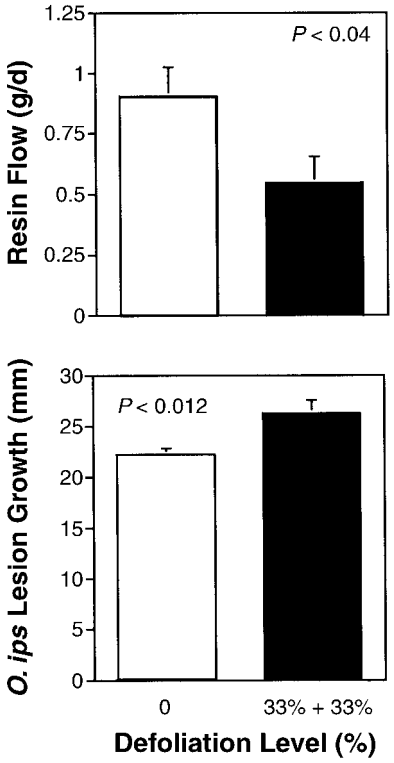

FIG. 4. Effect of defoliation on *Pinus resinosa* resistance against a stem-colonizing bark beetle–fungal complex. Two parameters of tree resistance remained suppressed 2 yr after defoliation.

twigs ($t_{17} = 2.669$; $P < 0.02$). However, feeding on 2-yr-old twigs was unaffected by treatment ($t_{17} = 1.104$; $P > 0.2$). Defoliation did not significantly affect oviposition ($P > 0.8$).

DISCUSSION

Defoliation altered the long-term suitability of *P. resinosa* to diverse insects feeding on different plant parts. Defoliation usually resulted in increased suitability to herbivores. For example, defoliation levels of ≥50% increased the performance of leaf feeding sawflies larvae (Table 2, Fig. 2) and stem colonizing beetles (Figs. 4, 5) 1 and 2 yr after defoliation. The only evidence of any reduced suitability to herbivores occurred at 33%, in which female sawfly cocoon size was smaller than in controls. In general, these results support the view of minimal between-year elevated resistance in evergreen trees following defoliation.

Responses to defoliation were quite complex. Among both the sawflies and beetles, certain parameters of host suitability varied with defoliation, whereas others did not. Likewise, when multiple defoliation intensities were administered, no simple linear relationships were observed. Nonlinear responses by herbivores to abiotic plant stresses, including soil nutrient and water deficiencies, have also been reported (Mattson and Haack 1987, English-Loeb 1989, Herms and Mattson 1992, Louda and Collinge 1992, Mopper and Whitham 1992).

The observed patterns of folivore performance may reflect nonlinear alterations in underlying plant physiological processes. In a subsample of these same seedlings, net photosynthesis, leaf conductance, and growth rate responded to defoliation intensity in a quadratic fashion (Reich et al. 1993). The reduced female sawfly cocoon mass observed at the 33% defoliation intensity corresponded with peak photosynthesis. However, the mechanism for these altered insect responses is unclear. Reduced photosynthesis can reduce the carbohydrate resources available for allelochemical production (Krause et al. 1993, Klepzig et al. 1995, 1996), but this explanation seems unlikely here. Foliar allelochemicals did not reduce *Neodiprion* larval development or cocoon mass in this or related studies (Larsson et al. 1986, Bjorkman and Gref 1993). Likewise, foliar nutrient compositions were generally quite stable, considering the wide range of treatments, although minor changes are known to sometimes have strong impacts on insect nutritional ecology (Clancy et al. 1988, Boecklen et al. 1991).

Previous studies indicate that effects of host age on suitability to herbivores can be either positive (Niemela et al. 1980, Perry and Pittman 1983) or negative (Karban 1987). In this study, defoliation treatments induced generally similar, although not entirely consistent, responses between seedlings and young trees. *N. lecontei* larval growth rate increased significantly on *P. resinosa* seedlings that were defoliated 50–75%, which corresponds to moderate increases in sawfly cocoon mass and reproductive effort on trees that were defoliated 66%. In those cases where seedlings and 10-yr-old trees did not show identical trends, the higher variation inherent in field studies, such as the block effects in foliar nutrients, seems the most likely explanation. For example, *N. lecontei* population outbreak behavior and

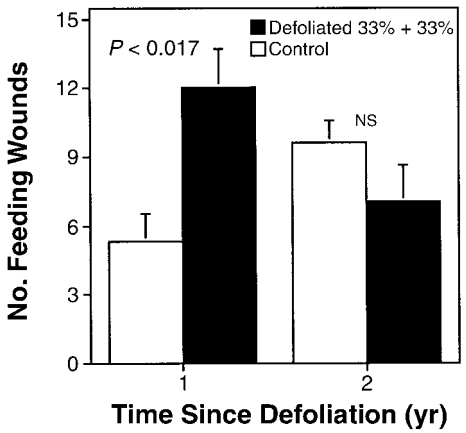

FIG. 5. Effects of defoliation and time since defoliation on suitability of *Pinus resinosa* to adult feeding by the root weevil *Hylobius pales.* Assays were conducted 1 and 2 yr after treatment.

host response appear similar among 5-, 8-, and 9-yr-old *P. resinosa* plantations (Averill et al. 1982).

Sixty-six percent defoliation increased the suitability of *P. resinosa* to stem- and root-colonizing Coleoptera over a period of two years. Since leaves are principally carbon sources that directly regulate carbohydrate allocation throughout a plant (Dickson and Isebrands 1991), defoliation of conifers can significantly reduce the carbon : nutrient balance and carbohydrate pool for growth and defense. This interpretation is consistent with work by Vanderklein and Reich (Submitted), showing that defoliation of *P. resinosa* reduces whole plant starch concentrations. Likewise, defoliation increased the suitability of grand fir, *Abies grandis* (Douglas) Lindley, to the fir engraver, *Scolytus ventralis* LeConte by reducing stem carbohydrate concentrations necessary for production of repellent monoterpenes (Wright et al. 1979).

The mechanisms by which multiple, simultaneous or sequential, stresses can interact to affect host suitability remains a major gap in our understanding of plant–herbivore relationships (Mooney et al. 1991, Sharpe and Rykiel 1991, Mopper and Whitham 1992, Krause et al. 1993, Sanchez-Martinez and Wagner 1994). Our results support the hypothesis that moderate sustained stress can improve insect folivore performance (Mopper and Whitham 1992), particularly in conifers. In the case of the *N. lecontei–P. resinosa* interaction, this response could result in continued herbivore pressure. During the early phases of population increase, oviposition is often highly clustered on a few trees despite the availability of adjacent, apparently healthy trees (Genys and Harman 1976, Krause 1994). Oviposition is particularly concentrated among trees showing signs of previous defoliation (Codella and Raffa 1995*a*). If individuals that fed on previously defoliated trees have relatively higher egg loads per unit of body mass as suggested here, that could further concentrate oviposition and feeding by reducing dispersal. The consequences of such cumulative stresses can be extremely high defoliation, reduced plant growth (Krause and Raffa 1996), and improved host suitability for opportunistic herbivores.

These results may relate to a complex decline syndrome currently affecting *P. resinosa* in the Great Lakes region (Klepzig et al. 1991). The epidemiology of this decline is not entirely characterized, but it is known that feeding by root- and stem-colonizing beetles is a critical component. Colonization of roots by *Hylobius–Leptographium* complexes reduces subsequent host defenses against lethal *I. pini–O. ips* complexes (Klepzig et al. 1995, 1996, Raffa and Klepzig 1996). Our current results suggest that defoliation by insect herbivores may be an important predisposing factor to these agents. Defoliation stress has been associated with several chronic declines of deciduous and evergreen tree species (Houston 1992, Manion and Lachance 1992). However, controlled long-term studies are lacking. An improved understanding and quantification of the relationships among foliage-, root-, and stem-feeding insects could contribute to our knowledge of factors inciting forest declines.

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